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Was extinction of New Zealand's avian megafauna an unavoidable consequence of human arrival?

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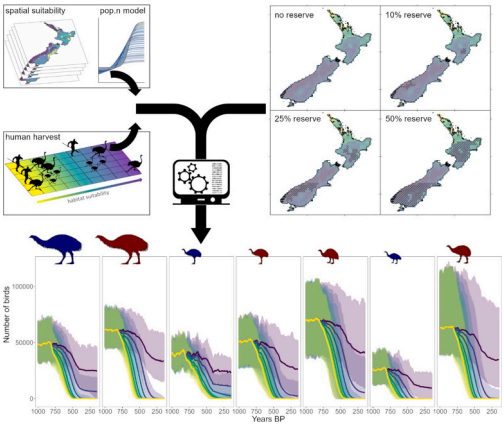
HIGHLIGHTS

- New Zealand's giant, flightless moa disappeared rapidly following arrival of humans.
- Using process-explicit ecological models, we test if these extinctions were avoidable.
- Moa persistence was not compatible with even low rates of hunting.
- Extinctions were avoided only if $\geq$ 50 % of land was protected from hunting.
- Our simulation method is useful for examining sustainable hunting rates of megafauna.

GRAPHICAL ABSTRACT



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ABSTRACT

Human overexploitation contributed strongly to the loss of hundreds of bird species across Oceania, including nine giant, flightless birds called moa. The inevitability of anthropogenic moa extinctions in New Zealand has been fiercely debated. However, we can now rigorously evaluate their extinction drivers using spatially explicit demographic models capturing species-specific interactions between moa, natural climates and landscapes, and human colonists. By modelling the spatial abundance and extinction dynamics of six species of moa, validated

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New Zealand
No-take zones
Process-based modelling
Spatially explicit population models
Sustainable harvest

against demographic and distributional inferences from the fossil record, we test whether their extinctions could have been avoided if human colonists moderated their hunting behaviours. We show that harvest rates of both moa birds (adults and subadults) and eggs are likely to have been low, varying between 4.0–6.0 % for birds and 2.5–12.0 % for eggs, annually. Our modelling, however, indicates that extinctions of moa could only have been avoided if Polynesian colonists maintained unrealistically expansive no-take zones (covering at least half of New Zealand's land area) and held their annual harvest rates to implausible levels (just 1 % of bird populations per annum). Although too late for moa, these insights provide valuable lessons and new computational approaches for conserving today's endangered megafauna.

1. Introduction

One of the hallmarks of today's global biodiversity crisis is declining abundances and continuing extirpations of Earth's largest vertebrates, the megafauna (Ripple et al., 2019). The loss of these iconic mammals, birds, and reptiles with adult body masses >40 kg is largely seen as a human-driven phenomenon (Ripple et al., 2019), which traces back from the earliest waves of hominid expansion to contemporary times (Johnson et al., 2017; Wallace, 1876). Past extinctions of megafauna on many continents and islands are primarily attributed to overharvesting, which, along with habitat loss and fragmentation, continue to pose significant threats to today's extant megafauna (Martin, 1984; Ripple et al., 2019). This simplification of megafaunal assemblages continues to have wide-reaching effects on ecosystem services, including the disruption of food web structures and destabilising the ecological processes mediated by these species (Amir et al., 2022; Estes et al., 2011).

Debate continues over the susceptibility of surviving megafauna to alternative harvesting strategies. Many megafaunal species, particularly those with low reproductive rates, may require the complete cessation of human harvesting to ensure their persistence (Clapham et al., 1999; Lusseau and Lee, 2016). Populations of other megafaunal species can be maintained through flexible, empirically informed systems of managed harvesting (Boyce et al., 2012; Cowlishaw et al., 2005; Miller, 1990). However, in most cases, successful conservation requires that limited harvests are complemented by the establishment of 'no-take' zones, often benefitting non-target, as well as target, species (Hendrick, 2009; Lum and Min, 2021). Such harvest-closure systems are common practice, but are not a modern concept. Traditional resource management techniques, embedded in ceremonies, religion, and other traditions, may have provided benefits similar to contemporary no-take zones and adaptive management (Bennett and Robinson, 2000; McClanahan et al., 2006).

Interventions for the recovery of endangered megafauna (and plants and other animals) are generally implemented when population sizes and distributional extents have declined so much that species are threatened with imminent extinction (Caughley, 1994). However, owing to extensive time-lags in demographic and ecological processes (Fordham et al., 2022), pathways to extinction can begin long before the latter stages of range collapse and population decline. Understanding and mitigating causes of population decline in its early stages, therefore, requires detailed knowledge of historical or even ancient drivers of population decline (Kuussaari et al., 2009; Tomlinson et al., 2022). Thus, there is a need to understand past harvest rates of megafauna to assess their ecological consequences, and to then apply these lessons to sustainably managing our remaining large-bodied animals (Bunnefeld et al., 2011).

Fortunately, ecologists and conservation biologists now have an impressive toolset with which to analyse the demographic and distributional dynamics of megafaunal species, including the effects of ancient harvesting, in many cases accurately modelling population declines long before they become critically endangered (Canteri et al., 2022; Lima-Ribeiro and Diniz-Filho, 2017; Pilowsky et al., 2023). These process-driven approaches (Pilowsky et al., 2022a) can reconstruct ecological dynamics and identify the drivers that caused past population declines and range contractions (Canteri et al., 2022; Fordham et al., 2022; Pilowsky et al., 2022b). Spatially explicit population models (SEPMs; (Fordham et al., 2021)) are a process-explicit approach with substantial promise in this regard, providing high-resolution estimates of the spatiotemporal dynamics of populations, habitats, and climatic conditions in response to diverse natural and anthropogenic drivers (Fordham et al., 2013; Tomlinson et al., 2022).

The islands of the Pacific Ocean once represented an especially biodiverse region of the world (Steadman, 1995). However, they were heavily impacted following colonisation and expansion of humans, who in the late Holocene embarked on extraordinary sea voyages, rapidly settling some of the most isolated landmasses on the planet (Blackburn et al., 2004; Duncan et al., 2013; Steadman, 1995; Wilmshurst et al., 2011). Polynesian colonisation of New Zealand was part of the final stage of this expansion, causing arguably one of the greatest losses of native species across the Pacific (Duncan and Blackburn, 2004; Wood et al., 2017). This included rapid extinction of all nine species of New Zealand's moa within 300 years following initial human arrival, and at least two centuries before European settlement of New Zealand in the early 19th century (Perry et al., 2014; Tomlinson et al., 2024a).

While climate fluctuations contributed to the extinctions of other charismatic megafauna (Fordham et al., 2022, 2024), the climate in New Zealand was relatively stable through the late-Holocene when Moa went extinct (Supplementary Fig. 1). Thus, humans not climate change (or their interaction) are blamed for extinctions of moa (Rawlence et al., 2012; Tomlinson et al., 2024a). Indeed it is often argued that the extinction of the large, flightless moa (ratites, Aves: Palaeognathae: Dinornithidae) was driven by relatively low rates of harvesting (Anderson, 1989; Holdaway et al., 2014; Holdaway and Jacomb, 2000; Perry et al., 2014), leading some to assert that these birds were doomed to extinction once the islands were colonised by humans (Anderson, 1983; Duncan et al., 2002). However, until now, this hypothesis has been difficult to test, largely because of a lack of high-resolution information on early human colonisation patterns across New Zealand (Anderson, 1991; Walter et al., 2017), and the absence of a rigorous, process-oriented methodology to establish the ecological impacts of that colonisation.

Recently, we have seen development of process-driven reconstructions of patterns of human colonisation of New Zealand at fine spatiotemporal scales (Tomlinson et al., 2024b), thus enabling the mechanisms responsible for the population decline and range contraction of its avifauna to be disentangled (Tomlinson et al., 2024a). Here we apply these methods to directly test whether extinctions of New Zealand's iconic moa were an inevitable consequence of human migration and colonisation (Duncan et al., 2002; Holdaway and Jacomb, 2000). We do this by developing and simulating counterfactual alternatives to established interactions between moa and humans (Tomlinson et al., 2024a), including tests of whether establishing no-take refugia could have prevented extinctions. Our findings provide important insights into the demographic sensitivity of moa, along with many other megafauna, to sustained, low levels of harvest. While such insights cannot resurrect moa, the methods and models developed provide valuable tools and insights for conserving today's remaining megafauna (Ford et al., 2017; Ripple et al., 2016).

2. Materials and methods

We used process-explicit models of moa-human-climate dynamics for six focal species of moa (*Dinornis robustus* and *D. novaezealandiae*, *Euryapteryx curtus*, *Megalapteryx didinus* and *Pachyornis elephantopus* and *P. geranoides*), which had been validated against inferences of demographic change from an extensive fossil record (Tomlinson et al., 2024a), to simulate competing scenarios of moa-human interactions at high spatiotemporal resolutions (Fig. 1). Thus, we applied these models to different scenarios of harvest rates and no-take harvest zones to determine the hunting and management practices that would have been necessary to maintain persistent populations of moa.

Spatially explicit population models (SEPMs), such as those developed to reconstruct the range collapse and extinction of moa (Tomlinson et al., 2024a) are highly suited to exploring 'counterfactual' scenarios - plausible alternatives to what occurred historically (Pilowsky et al., 2022a). They have been used previously to establish the dynamic interplay of climate and humans in driving population declines, range contractions and subsequent extinctions that happened thousands of years ago (Canteri et al., 2022; Fordham et al., 2022; Pilowsky et al., 2022b). In our counterfactual scenarios, we used SEPMs to test whether reduced harvesting by humans could have allowed moa to persist into the 1800s, beyond the time of the first arrival of Europeans in New Zealand in 1769 (Pool, 1991). We did not test alternative no-climate change scenarios, as has been done elsewhere (Fordham et al., 2022; Pilowsky et al., 2022b), because moa extinctions were predominantly human-driven, with no substantive effect of climatic change (Rawlence et al. (2012); Supplementary Fig. 1). The approach, including scenario development, simulation and post-hoc analysis is described in detail in the Supplementary Methods. It is supported by Program R code for model development and analyses (Tomlinson and Fordham, 2024).

2.1. Human colonisation patterns

The peopling of New Zealand was simulated using a process-explicit modelling technique that integrates archaeological data with a SEPM of population growth and dispersal dynamics (Tomlinson et al., 2024b). This model accurately reconstructs Polynesian populations at European arrival in New Zealand in 1769, and it provides associated inferences of colonisation and expansion at a spatiotemporal resolution that most other models cannot. In this model, arrival, population growth and spread of human colonists across New Zealand are reconstructed at annual time steps between 450C.E. – 1800C.E. (the latter date approximating European settlement). Each step is conditioned by (i) paleoclimatic conditions, including annual rainfall (mm) and the average temperature (°C) for the coldest and warmest three-month periods; and (ii) by environmental factors, including slope and distance to the coast. To capture likely uncertainty in human hunting pressures on moa, we generated 10,000 different models of human population growth and dispersal across New Zealand by exhaustively sampling the optimised parameter space (Tomlinson et al., 2024b), equally treating each model as a likely reality (Fordham et al., 2022; Tomlinson et al., 2024a).

2.2. Moa-human-climate interactions

The range collapse and eventual extinction of six species, including two subspecies, of moa (*D. robustus*, *D. novaezealandiae*, *E. curtus curtus* and *E. curtus gravis*, *M. didinus*, *P. geranoides* and *P. elephantopus*) were reconstructed using spatially-explicit population models (SEPM) with pattern-oriented model (POM) validation (Tomlinson et al., 2024a). Using female-only age-structured matrix population models with a lattice-type spatial framework, these models simulated moa-human-climate interactions at a high spatiotemporal resolution (annually at 50 km × 50 km from 450 to 1850 CE). The carrying capacity of each cell varied between SEPMs and through time in response to a modelled

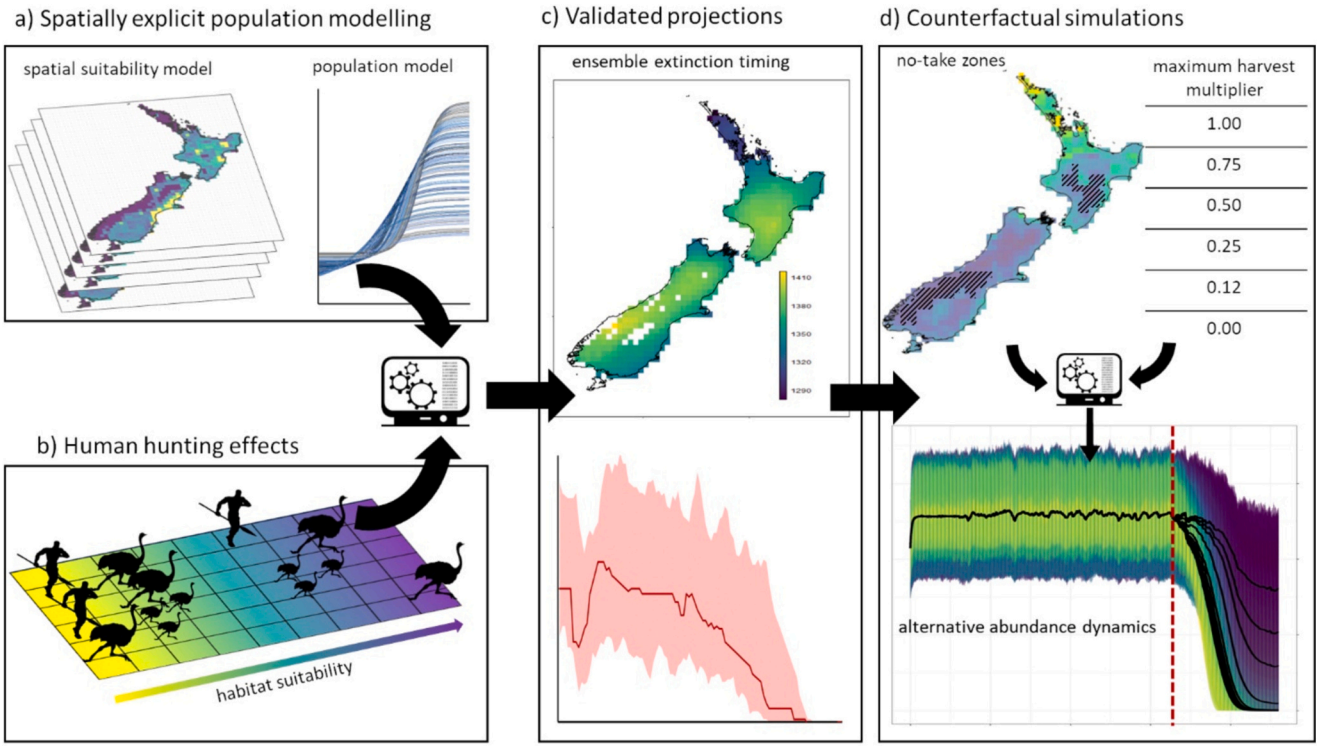

Fig. 1. Reconstructing exploitation of moa by humans. The framework involves a) integrating spatially explicit population models with b) spatiotemporal simulations of human expansion across the landscape and subsequent harvesting pressure to generate c) spatiotemporal projections of occurrence, abundance, dispersal and harvest that reconstruct inferences of range contraction and extinction consistent with the fossil record. These validated models can be used to conduct d) *in silico* experiments of the biological consequences of different rates of harvesting after human arrival (red dashed line) using counterfactual scenarios.

approximation of the realised niche and upper moa abundance (Fordham et al., 2022), with the former being conditioned by paleoclimatic patterns of annual rainfall, temperature extremes and geomorphology. Survival and fecundity rates were based on published estimates (Holdaway and Jacomb, 2000), modified for interspecific differences in age at sexual maturity (Turvey et al., 2005). Density-dependent population growth was modelled according to a logistic function (Ricker, 1954) and dispersal distances were estimated allometrically (Sutherland et al., 2000). The latter allowed the proportion of dispersers to vary across large but plausible ranges. Hunting was modelled as a function of the timing of the arrival and abundance of humans in a given grid cell (Tomlinson et al., 2024a, 2024b) and was dependent on prey density and availability (Alroy, 2000; Canteri et al., 2022; Fordham et al., 2022; Pilowsky et al., 2022b). To account for uncertainty in demographic parameters and environmental attributes, hundreds of thousands of unique iterations of the model were parameterised using Latin hypercube sampling (McKay et al., 1979; Norton, 2015). These models were evaluated against inferences of demographic change from the fossil record using POM (Grimm and Railsback, 2012). This validation method identified models that accurately simulated likely interspecific differences in spatiotemporal occurrence and timing of extinction based on the fossil record (Signor et al., 1982).

2.3. Counterfactual scenarios

To explore the biological consequences of harvesting on moa extinction dynamics, we conducted *in silico* experiments using SEPMs with validated estimates of ecological, demographic and harvest parameters (Dataset S2) based on POM (Fordham et al., 2020). We reconstructed moa spatiotemporal abundance and their harvest impacts using 100 unique models for each species. We used Latin hypercube sampling (McKay et al., 1979; Norton, 2015) of upper and lower confidence bounds to ensure a representative coverage of parameter uncertainty (Tomlinson et al., 2024a) and counterfactual scenarios to alter 'best estimates' of interactions between Polynesian colonists and moa populations. Specifically, we tested whether reducing harvest rates of birds (aged ≥1 year) and eggs (aged <1 year) could have enabled moa to persist beyond the arrival of Europeans in New Zealand in 1769. This involved sequentially reducing harvest rates by 5 to 100 % from the empirical rate of harvest required to reconcile inferences of range and extinction dynamics from the fossil record using POM techniques (Tomlinson et al., 2024a). A full list of counterfactual harvest rate scenarios is shown in Dataset S2 (and Supplementary Fig. 5). They included sequential reductions in bird harvesting under scenarios where egg harvesting was either retained or prevented. Therefore, scenarios where no birds were harvested could still result in human-driven population declines for scenarios where egg harvesting was maintained.

We used an analogous counterfactual approach to test whether no-take zones could have prevented the extinction of moa. Traditional hunting practices around the world often incorporate social guidelines or taboos that impose sustainability by preventing or limiting harvest of some species at some times and places (Bennett and Robinson, 2000; Cinner et al., 2005). While there is no evidence that hunting of moa by humans was limited in time or space by cultural practices, the question of whether the extinction of moa could have been avoided had human colonists established no-take areas (Polynesian '*rāhui*'), remains valuable. To do this, we identified areas for *rāhui* that were most marginal for humans based on their climate and environmental preferences (Tomlinson et al., 2024b). The rationale behind this decision was that contemporary areas reserved for conservation are often those that are least useful to people (Venter et al., 2018). To test the possible efficacy of *rāhui*, we identified areas of New Zealand with grid cells of low to medium suitability for human colonists using high-resolution reconstructions (Tomlinson et al. (2024b); Supplementary Fig. 4). We used the "adjacent" and "clump" algorithms in the *raster* package (Hijmans, 2020) to retain the largest contiguous area for the lowest 10 %, 20 % and 50 % of area suitable to humans on each island. These levels corresponded to simulated *rāhui* that spanned approximately 5 %, 15 %, and 50 % of the land area of New Zealand, respectively.

2.4. Statistical analyses

For each counterfactual simulation, we calculated the percentage of the population of birds (aged ≥1 year), and the percentage of eggs (aged <1 year) harvested every year. We used these harvest values to estimate the average and maximum offtake percentages during the interval between Polynesian and European arrival for each species under each counterfactual scenario. We also calculated extinction risk under different harvest scenarios by calculating expected minimum population size (McCarthy and Thompson, 2001) and proportional population decline between time of arrival of Polynesians in New Zealand and the end of the simulation (1800 CE). To calculate the second of these extinction metrics, we compared the mean number of individuals of each species that were present in the 100 years prior to human colonisation (pre-human population) and those in the decades immediately prior to and after European contact with New Zealand in (1700–1800 CE).

We conducted a global sensitivity analysis to identify the relative contributions of variable parameters to simulation outputs (Si et al., 2020) using a Bayesian linear method in the 'rstanarm' package for R (Muth et al., 2018). All variable model parameters were regressed against the Euclidean distance from an idealised model. This approach identified which model parameters had the largest influence on minimising the Euclidian distance between simulated and inferred demographic change. Models for sensitivity analysis were constructed with informed priors (Tomlinson et al., 2024a), each with 10,000 samples. We ensured model convergence using Gelman-Rubin statistics (where values less than or equal to 1.1 were considered acceptable), along with testing for effective sample size, and visually examining trace-plots (Fordham et al., 2024).

3. Results

3.1. Rates of harvest and population decline

Populations of all moa taxa are most likely to have been large and stable for centuries prior to colonisation of New Zealand by Polynesians (Fig. 2). These population abundances declined immediately after the arrival of people in New Zealand due to the harvesting of birds and eggs in our simulations, leading to the first species extinctions of moa in as little as 100 years, with all birds likely to have gone extinct within 300 years of human arrival in New Zealand (Fig. 2). These extinctions probably resulted from average annual rates of population decline that ranged from 2.0 ± 0.2 % for *E. curtus curtus* to 3.7 ± 0.2 % for *P. geranoides*, with maximal rates (during their extinction trajectories) of 7.6 ± 1.2 % to 13.3 ± 2.3 % for these species, respectively (Supplementary Fig. 5).

Bird harvesting is likely to have been highest for *D. novaezealandiae* (6.0 ± 0.1 % of the population annually), and lowest for *E. curtus curtus* (4.0 ± 0.0 % of the population annually), with estimated maximal annual rates of harvest ranging between 7.2 ± 0.4 % for *E. curtus curtus* and 15.2 ± 0.1 % for *D. robustus*. Interspecific variation in egg harvesting is likely to have been higher than for bird harvesting, with egg harvest rates ranging from 2.5 ± 0.1 % to 12.0 ± 0.4 % of total eggs per annum for *D. robustus* and *E. curtus curtus*, respectively (Supplementary Fig. 2). Egg harvest during periods of heaviest exploitation, however, ranged from 4.7 ± 0.2 % for *P. geranoides* to 32.7 ± 1.6 % for *E. curtus curtus* (Fig. 2).

Our global sensitivity analysis showed that harvesting birds rather than eggs had the strongest influence on range contraction and extinction; this based on inferences from the fossil record (relative importance values of harvesting adult vs. eggs was 1.56 vs. 0.49, respectively;

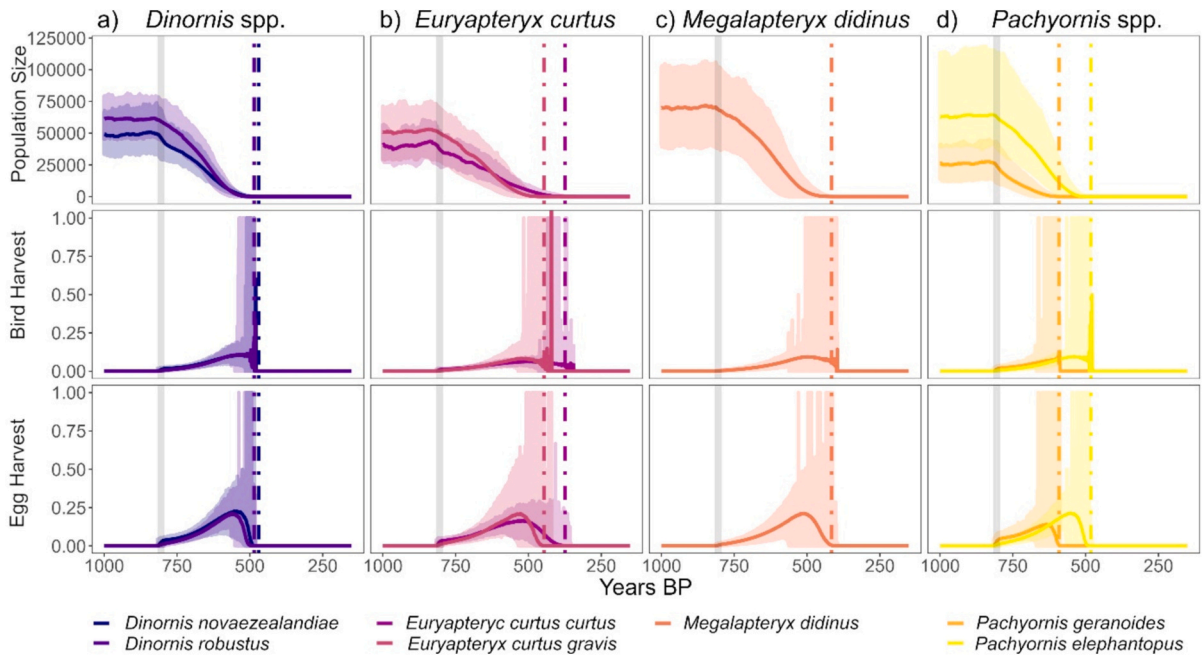

Fig. 2. Population size and proportion of total birds and eggs harvested. Solid line shows the ensemble mean estimate based on the subset of "best" spatially explicit population models (SEPMs). Pale shaded areas indicate the range of values generated by these 'best' SEPMs. The grey vertical line shows time of human arrival in New Zealand, while vertical dashed lines indicate the simulated time of extinction.

Supplementary Fig. 3).

3.2. Effects of reduced harvesting

Our modelling indicated that the extinction of moa was likely unavoidable even at low levels of bird harvesting (Fig. 3). Counterfactual scenarios showed that the extinction of most moa could only have been avoided if bird harvesting was limited to levels of <10 % of likely annual offtake (i.e., scenarios with >90 % reduction in actual harvest rates). However, even these highly reduced levels of bird harvesting rendered the remaining populations precariously low in abundance and, thus, highly prone to extinction (Fig. 3).

We detected substantial differences in susceptibility of moa species to harvest. Our simulations estimate that reducing bird harvest rates by 90 % would have resulted in population declines of 94.7 ± 7.3 % for *E. curtus gravis*, 91.0 ± 10.8 % for *M. didinus*, 86.4 ± 9.4 % for *D. novaezealandiae*, and 71.1 ± 8.0 % for *E. curtus curtus* (Fig. 3). Our modelling indicated that only *E. curtus curtus* would have potentially avoided extinction if harvest rates were held at just 25 % of likely rates, with this species persisting at abundances of only 7.7 ± 6.7 % of their pre-human levels. In contrast, we project that extinction of *D. robustus*, *P. geranoides* and *P. elephantopus* would have occurred by the 1800s even if bird harvesting was reduced by 90 % (Fig. 3).

In the absence of egg harvesting, extinction risk from scenarios with a 90 % reduction remained high for most species (Supplementary Fig. 5). Conversely, in the complete absence of bird (adult and subadult) harvesting, likely egg harvest rates of 37–46 % (Tomlinson et al., 2024a) would not alone have caused the extinction of any species of moa. However, egg harvesting (without bird harvesting) would have reduced populations of moa by 40–60 % by the time of European arrival (Fig. 3 – scenario with no bird harvesting).

3.3. Effects of no-take zones

In scenarios with *rāhui* and no reduction in harvest rates, proportional population declines (i.e., loss of individuals relative to pre-human abundances) for all species remained high and expected minimum abundance remained precariously low unless *rāhui* encompassed c. 50 % of the land area of New Zealand; this located in habitats least favoured by human colonists (Fig. 4). With *rāhui* covering 50 % of the archipelago, minimum moa population sizes were approximately 20,000 individuals (c. 25 % of the pre-human population) for all species at the time of European arrival (Fig. 4). Even under these scenarios (50 % *rāhui*), however, *P. geranoides* would likely have gone extinct by approximately 1624 CE because it was limited to the smallest area of high-suitability habitat, the smallest fraction of optimal habitat being protected by *rāhui* (Supplementary Fig. 4), and its individuals dispersed further than most other moa species (Tomlinson et al., 2024a), increasing their likelihood of leaving *rāhui* and being harvested.

Our simulations showed that without being complemented by reduced harvesting pressure, *rāhui* alone could not have prevented dramatic population declines for most species (Fig. 4). In scenarios where *rāhui* were maintained across c. 50 % of New Zealand, harvest rate for *D. novaezealandiae* and *E. curtus curtus* needed to be reduced by ≥50 % for their populations to persist at levels of at least half of their pre-human population sizes (Fig. 4). For *D. robustus*, *E. curtus gravis*, *M. didinus*, *P. geranoides* and *P. elephantopus*, reductions in harvest rates of ≥90 % were needed to maintain population levels of at least half of their pre-human sizes (Fig. 4).

Reserving ≤20 % of New Zealand as *rāhui* resulted in population losses that exceeded 50 % of pre-human abundance for all species, even when harvest rates outside *rāhui* were held at <10 % of likely harvest rates (Fig. 4). Under the 20 % *rāhui* scenario, reduction in annual harvest rates by as much as 90 % still resulted in populations persistence ranging from just 1 % (*P. geranoides*) to 44 % (*E. curtus curtus*) of pre-human abundances, with expected minimum abundances ranging from 294 ± 92 to 18,009 ± 877 in these species, respectively (Fig. 4; Dataset S2). Proportional population declines and minimum population abundance under a 5 % *rāhui* scenario remained very similar to those simulated without *rāhui*.

4. Discussion

Overexploitation by first human settlers resulted in the loss of hundreds of bird species across Oceania (Blackburn et al., 2004; Duncan et al., 2013), including an entire guild of avian megafauna from New

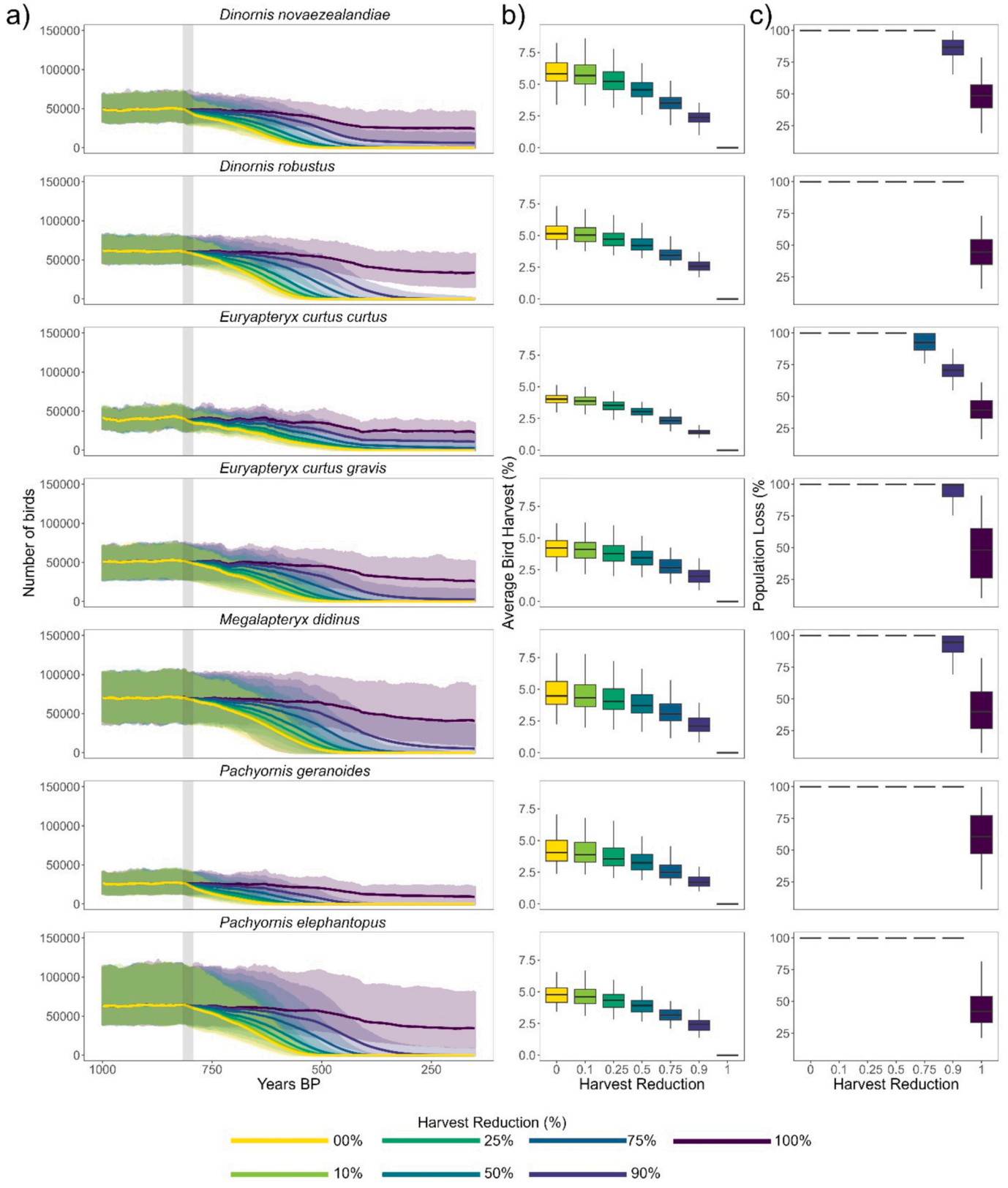

Fig. 3. Effects of reducing bird harvest rates on moa populations. a) Population trajectories for seven moa taxa in response to baseline (best estimates) harvest rates (0 % harvest reduction) and six counterfactual harvest rates (10 to 100 % reduction). The shaded bounds represent the range of population sizes simulated by 100 models (representing likely parameter space (Tomlinson et al., 2024a)) under each scenario. In all scenarios, eggs are harvested at best estimate rates described in Supporting Table 2. The grey vertical band shows the range of likely human arrival dates used in these simulations. b) Relationship between percentage of birds exploited and harvest reduction scenario. c) Effect of harvest reduction on percent reduction in population size at the time of European arrival in New Zealand. In each panel different colours represent responses to different harvest pressures, ranging from a 100 % reduction (purple), where no birds ≥1 year are harvested, to 0 % reduction (yellow) where best estimates of bird harvesting (based on POM) remain unaltered.

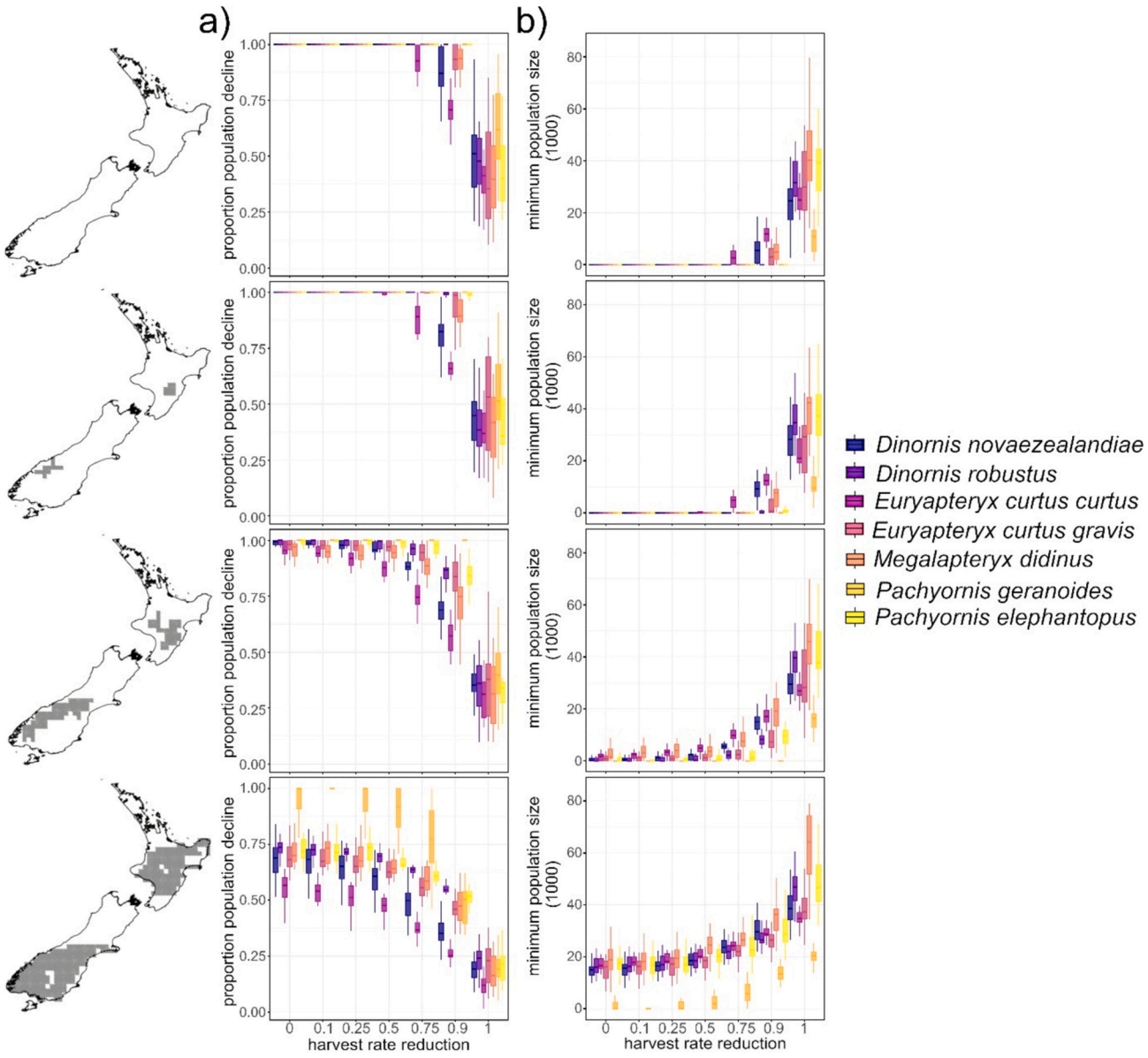

Fig. 4. Effects of *rāhui* (no-take zones) on moa extinction dynamics. Counterfactual scenarios for seven taxa of moa showing the combined effects of establishing *rāhui* and reducing harvest rates on two measures of extinction risk: (a) proportional change in population size from time of human arrival in New Zealand to the termination of the simulation (proportion population decline) and (b) expected minimum population size (in thousands). Each row shows results for counterfactual *rāhui* scenarios encompassing 0 %, 5 %, 15 % and 50 % of land area respectively. Maps show location of simulated *rāhui* in grey.

Zealand, consisting of nine species of moa (Holdaway et al., 2014; Holdaway and Jacomb, 2000; Perry et al., 2014; Tomlinson et al., 2024a). Here, using process-driven simulation models to test counterfactual harvesting scenarios, we show that the extinction of moa was inevitable once humans arrived and colonised New Zealand.

4.1. Population declines and extinction

We found that human harvesting of <6 % of moa (including juveniles, subadults and adults) annually resulted in extinctions after approximately 95–315 years of coexistence with humans, depending on the species. This finding is consistent with harvest theory for long-lived vertebrates (Fordham et al., 2008; Hilker and Liz, 2020), and knowledge of the demography of moa and other flightless birds around the world. It is likely that moa matured late (between 2 and 7 years (Turvey et al., 2005)), had long reproductive lives (up to or beyond 15 years for females (Holdaway and Jacomb, 2000; Turvey and Holdaway, 2005)), and high adult survivorship (Holdaway and Jacomb, 2000). This "slow" life history (Dobson and Oli, 2007) made them particularly sensitive to harvesting of adult birds (Turvey and Holdaway, 2005), as shown in our process-based simulations, where moa went extinct even under very low rates of harvesting of birds – a finding also asserted elsewhere using less computationally intensive methods (Holdaway et al., 2014; Holdaway and Jacomb, 2000; Perry et al., 2014). We also show that if only eggs were harvested by the first colonists, moa would have probably persisted, albeit in much smaller numbers then pre-human densities. These findings are consistent with emerging evidence that prehistoric megafaunal extinctions often resulted from low but sustained levels of hunting following first contact with humans (Fordham et al., 2022, 2024; Pilowsky et al., 2022b).

By tracing population histories of multiple taxa of moa at fine spatiotemporal resolutions, we established important interspecific differences in interactions between humans and moa. *Dinornis* spp. were likely to have been harvested most heavily, at rates of nearly twice those

of the smaller *E. curtus* and *P. geranoides*. This result stands in stark contrast to previous assertions (Kooyman, 1985), but it is entirely consistent with the general tendency for predators (humans or otherwise) to be highly selective in their choice of prey. Perhaps counterintuitively, the species most heavily harvested in our simulations (i.e., *Dinornis* spp.) were not the first to be driven to extinction. It is likely that species susceptibility is the product of interactions among species' traits and the spatiotemporal patterns of anthropogenic factors (Tomlinson et al., 2024a). For example, a small distribution overlapping largely with favourable landscapes for human colonisation, low growth rate, and low population abundance made *P. geranoides* particularly vulnerable to overexploitation.

While the rate of harvesting of moa eggs was likely to have been substantial (estimated at 2.5 to 12.0 % of available clutches), our simulations and sensitivity analysis indicate that moa extinctions were primarily driven by bird harvesting, as suggested elsewhere (Oskam et al., 2012). However, our counterfactual modelling approach also shows that even in the total absence of bird harvesting, egg harvesting would have resulted in large population declines. Declines of approximately 40 % of the pre-human population size were simulated even for species of moa with the lowest egg harvest rates (*E. curtus* and *M. didinus*). These substantial population declines probably reflect the low reproductive potential of female moa, which likely produced $\leq$1 egg annually (Werner and Griebeler, 2012). This is also consistent with male moa having protected only a single chick to maturity at a time (Diamond, 2000; Worthy and Holdaway, 1999), much like extant flightless birds such as cassowaries and kiwis do today (Calder, 1990; Romer, 1997).

The simulations that we have developed here exclusively reconstructed and manipulated patterns and rates of moa harvest by humans. There were, however, other drivers of ecological change following Polynesian colonisation of New Zealand that are likely to have contributed to moa population declines, such as increased fire frequency and changed vegetation structure (McGlone and Wilmshurst, 1999; Perry et al., 2012). Likewise, human commensal species may have also contributed to moa declines (Greig and Rawlence, 2021; Holdaway, 1999), but have been difficult to disentangle from the expanding influence of human colonists themselves.

4.2. No-take zones for conservation

No-take zones are a common conservation management tool (Maxwell et al., 2020; Possingham et al., 2006) with a long history, potentially spanning millennia (Ens et al., 2012), where traditional harvesting practices often incorporated prescriptions to disperse hunting pressures across the landscape (Robinson and Bennett, 1999). The establishment of protected areas, including no-take zones, in contemporary conservation management rests on the theory of metapopulation dynamics, where populations in protected areas provide an important source of individuals that can disperse into and supplement populations in surrounding areas (Maxwell et al., 2020; Possingham et al., 2006). For large-bodied animals, these reserves often need to be expansive to accommodate and circumscribe long-distance movements of focal species (Campbell et al., 2012; de Vires, 1995). Even for relatively small-bodied flightless birds, such as kiwi in New Zealand, large reserves are required to accommodate their substantial home ranges (Fraser et al., 2015).

Our simulations show that moa *rāhui* would have needed to be exceptionally large, covering >50 % of the New Zealand land area to prevent moa extinctions. This exceeds the current-day expanse of New Zealand's protected areas by a factor of 1.5 (here including the 32 % of New Zealand administered under Department of Conservation Estate, Nature Heritage Fund, Ngā Whenua Rāhui and QE II National Trust covenants for biodiversity conservation (Bingham et al., 2021; Craig et al., 2000)). Key to understanding this result is that no-take zones (*rāhui* or otherwise) are generally located in areas of marginal habitat – those less productive in supporting human populations and the crops and other resources upon which they depend (Fuller et al., 2010; Venter et al., 2018). In New Zealand, most species of moa are likely to have shared a similar affinity for warmer and drier lowland environments with Polynesian colonists (Latham et al., 2020; Tomlinson et al., 2024a, 2024b), meaning our simulated *rāhui* were located in landscapes with generally poor habitat quality for moa as well as people (Supplementary Fig. 4). Moreover, the mean natal dispersal distance for moa was between 15 and 30 km, with some species dispersing distances of as much as 80 km (Tomlinson et al., 2024a); thus, any no-take zones would have needed to have been exceptionally large to protect against high mortality of emigrants.

We suggest that protected areas for the world's surviving megafauna, including large, flightless birds, must be large, contiguous, and capture at least some high quality habitat, rather than only habitat that is least commercially valuable and often least ecologically suitable (Fuller et al., 2010; Venter et al., 2018). While the simulations and counterfactuals described here cannot reverse moa extinction, our model-based approach provides a method for identifying optimal protected area strategies for conservation that could be applied to other species. Nevertheless, even with an extensive protected area network, species management outside these areas must be intense to prevent broad-scale population declines.

5. Conclusions

Our simulations provide strong support for assertions that moa could not have persisted once humans, or any large mammalian predator, reached New Zealand. Indeed, the long-term survival of moa would have required harvest rates to be so limited, and *rāhui* to be so expansive that it would have precluded moa as viable sources of food. These retrospective insights may be too late for the extinct moa, but they demonstrate how process-based simulation models of the kind deployed here hold substantial promise for conserving the remaining species of flightless birds and other persisting megafauna.

Glossary

Counterfactual An experimental method to test the causal strength of an inferred relationship by reconstructing the scenario where a specific event did not happen, and evaluating the likelihood of the alternative conditions required to do so.

Pattern-oriented model (POM) A multi-criteria approach to selecting and calibrating models of complex systems, where statistical simulations are assessed by their capacity to reconstruct a multivariate target representing different empirical outcomes of complex interactions. The technique can be used to select the most accurate simulations, optimise them, and ideally identify key parameters underpinning their mechanism of operation.

Rāhui An East Polynesian cultural principle, commonly associated with Māori resource management and custodianship of the natural world, applied to restrict or prohibit the exploitation of specific resources at different times, or in specific locations. Used here to denote a traditional approach to the modern concept of no-take or non-harvest zones.

Spatially explicit population models (SEPMs) Models of population dynamics that incorporate real-world habitat complexity and represent spatially or spatiotemporally variable patterns in how individual populations may respond to different conditions.

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CRediT authorship contribution statement

Sean Tomlinson: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis. **Mark V. Lomolino:** Writing – review & editing, Funding acquisition, Conceptualization. **Jamie R. Wood:** Writing – review & editing, Validation, Methodology, Data curation. **Atholl Anderson:** Writing – review & editing, Methodology. **George L.W. Perry:** Writing – review & editing, Methodology, Data curation. **Janet M. Wilmshurst:** Writing – review & editing, Methodology, Data curation. **Jeremy J. Austin:** Writing – review & editing, Funding acquisition, Conceptualization. **Damien A. Fordham:** Writing – review & editing, Visualization, Validation, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization.

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Declaration of competing interest

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Data availability

All data and analysis code are available on FigShare at the link provided in the mauscript text.

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